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U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF ENTOMOLOGY—BULLETIN No. 121.
L. O. HOWARD, Entomologist and Chief of Bureau.

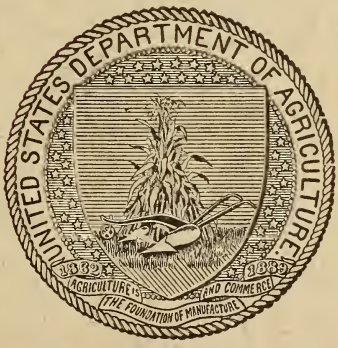
THE BEHAVIOR OF THE HONEY BEE IN POLLEN COLLECTING.

U.S. DEPT. OF AGRICULTURE
DEC - 1912

BY

D. B. CASTEEL, PH. D.,
Collaborator and Adjunct Professor of Zoology,
University of Texas.

ISSUED DECEMBER 31, 1912.



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D. B. Casteel, *collaborator.*

LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Entomology,
Washington, D. C., September 23, 1912.

Sir: I have the honor to transmit herewith a manuscript entitled "The Behavior of the Honey Bee in Pollen Collecting," by Dr. Dana B. Casteel, of this bureau. The value of the honey bee in cross pollinating the flowers of fruit trees makes it desirable that exact information be available concerning the actions of the bee when gathering and manipulating the pollen. The results recorded in this manuscript are also of value as studies in the behavior of the bee and will prove interesting and valuable to the bee keeper. The work here recorded was done by Dr. Casteel during the summers of 1911 and 1912 at the apiary of this bureau.

I recommend that this manuscript be published as Bulletin No. 121 of the Bureau of Entomology.

Respectfully,

L. O. Howard,
Entomologist and Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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THE BEHAVIOR OF THE HONEY BEE IN POLLEN COLLECTING.

INTRODUCTION.

While working upon the problem of wax-scale manipulation during the summer of 1911 the writer became convinced that the so-called wax shears or pinchers of the worker honey bee have nothing whatever to do with the extraction of the wax scales from their pockets, but rather that they are organs used in loading the pollen from the pollen combs of the hind legs into the corbiculæ or pollen baskets (Casteel, 1912). Further observations made at that time disclosed the exact method by which the hind legs are instrumental in the pollen-loading process and also the way in which the middle legs aid the hind legs in patting down the pollen masses. During the summer of 1912 additional information was secured, more particularly that relating to the manner in which pollen is collected upon the body and legs of the bee, how it is transferred to the hind legs, how it is moistened, and finally the method by which it is stored in the hive for future use. In the present paper a complete account will be given of the history of the pollen from the time it leaves the flower until it rests within the cells of the hive. The points of more particular interest in the description of pollen manipulation refer to (1) the movements concerned in gathering the pollen from the flowers upon the body and legs, (2) the method by which the baskets of the hind legs receive the loads which they carry to the hive, and (3) the manner in which the bee moistens pollen and renders it sufficiently cohesive for packing and transportation.

THE STRUCTURES CONCERNED IN THE MANIPULATION OF POLLEN.

The hairs which cover the body and appendages of the bee are of the utmost importance in the process of pollen gathering. For the purposes of this account these hairs may be classified roughly as (1) branched hairs and (2) unbranched hairs, the latter including both long, slender hairs and stiff, spinelike structures.

Of these two classes the branched hairs are the more numerous. They make up the hairy coat of the head, thorax, and abdomen, with the exception of short sensory spines, as those found upon the antennæ and perhaps elsewhere, and the stiff unbranched hairs which

cover the surfaces of the compound eyes (Phillips, 1905). Branched hairs are also found upon the legs; more particularly upon the more proximal segments. A typical branched hair is composed of a long slender main axis from which spring numerous short lateral barbs. Grains of pollen are caught and held in the angles between the axis and the barbs and between the barbs of contiguous hairs. The hairy covering of the body and legs thus serves as a collecting surface upon which pollen grains are temporarily retained and from which they are later removed by the combing action of the brushes of the legs.

Although, as above noted, some unbranched hairs are located upon the body of the bee, they occur in greatest numbers upon the more distal segments of the appendages. They are quite diverse in form, some being extremely long and slender, such as those which curve over the pollen baskets, others being stout and stiff, as those which form the collecting brushes and the pecten spines.

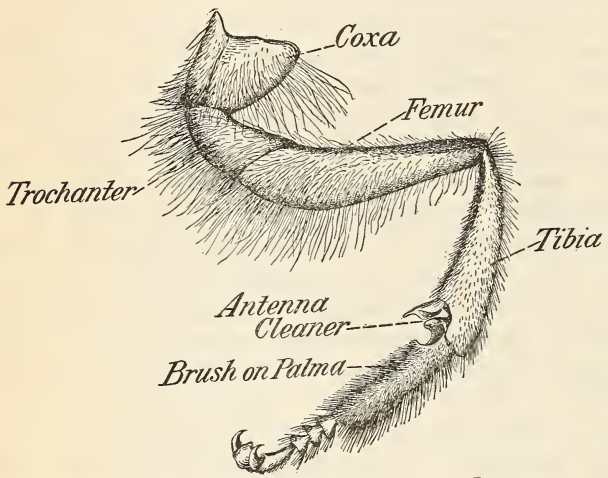

FIG. 1.—Left foreleg of a worker bee. (Original.)

The mouth-parts of the bee are also essential to the proper collection of pollen. The mandibles are used to scrape over the anthers of flowers, and considerable pollen adheres to them and is later removed. The same is true of the maxillæ and tongue. From the mouth comes the fluid by which the pollen grains are moistened.

The legs of the worker bee are especially adapted for pollen gathering. Each leg bears a collecting brush, composed of stiff, unbranched hairs set closely together. These brushes are located upon the first or most proximal tarsal segment of the legs, known technically as the palmæ of the forelegs and as the plantæ of the middle and hind pair. The brush of the foreleg is elongated and of slight width (fig. 1), that of the middle leg broad and flat (fig. 2), while the brush upon the planta of the hind leg is the broadest of all, and is also the most highly specialized. In addition to these well-marked brushes, the distal ends of the tibiæ of the fore and middle legs bear many stiff hairs, which function as pollen collectors, and the distal tarsal joints of all legs bear similar structures.

The tibia and the planta of the hind leg of the worker bee are greatly flattened. (See figs. 3, 4.) The outer surface of the tibia is marked by an elongated depression, deepest at its distal end, and bounded laterally by elevated margins. From the lateral boundaries of this depression spring many long hairs, some of which arch over the concave outer surface of the tibia and thus form a kind of receptacle or basket to which the name corbicula or pollen-basket is given. The lower or distal end of the tibia articulates at its anterior edge with the planta. The remaining portion of this end of the tibia is flattened and slightly concave, its surface sloping upward from the inner to the outer surface of the limb. Along the inner edge of this surface runs a row of short, stiff, backwardly directed spines, from 15 to 21 in number, which form the pecten or comb of the tibia. The lateral edge of this area forms the lower boundary of the corbicular depression and is marked by a row of very fine hairs which branch at their free ends. Immediately above these hairs, springing from the floor of the corbicula, are found 7 or 8 minute spines, and above them one long hair which reaches out over the lower edge of the basket.

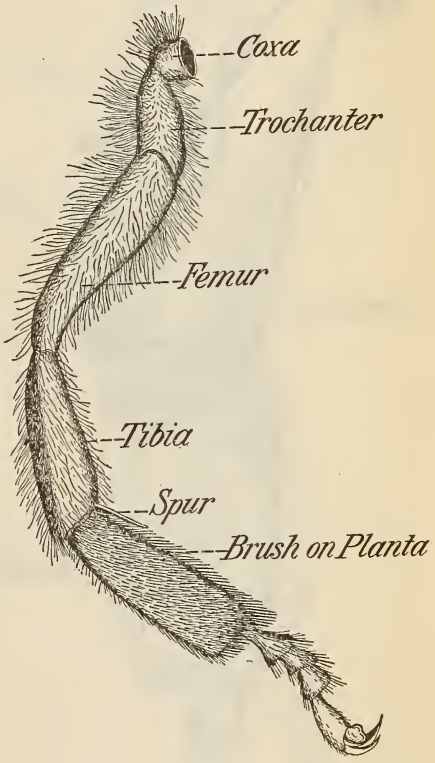

FIG. 2.—Left middle leg of a worker bee. (Original.)

The broad, flat planta (metatarsus or proximal tarsal segment of the hind leg) is marked on its inner surface by several rows of stiff, distally directed spines which form the pollen combs. About 12 of these transverse rows may be distinguished, although some of them are not complete. The most distal row, which projects beyond the edge of the planta, is composed of very strong, stiff spines which function in the removal of the wax scales (Casteel, 1912). The upper or proximal end of the planta is flattened and projects in a posterior direction to form the auricle. The surface of the auricle is marked with short, blunt spines, pyramidal in form, and a fringe of fine hairs with branching ends extends along its lateral edge. This surface slopes upward and outward.

THE POLLEN SUPPLY.

When bees collect pollen from flowers they may be engaged in this occupation alone or may combine it with nectar gathering. From some flowers the bees take only nectar, from others only pollen; a third class of flowers furnishes an available supply of both of these substances. But even where both pollen and nectar are obtainable a bee may gather nectar and disregard the pollen. This is well illustrated by the case of white clover. If bees are watched while working upon clover flowers, the observer will soon perceive some which bear pollen masses upon their hind legs, while others will continue to visit flower after flower, dipping into the blossoms and securing a plentiful supply of nectar, yet entirely neglecting the pollen.

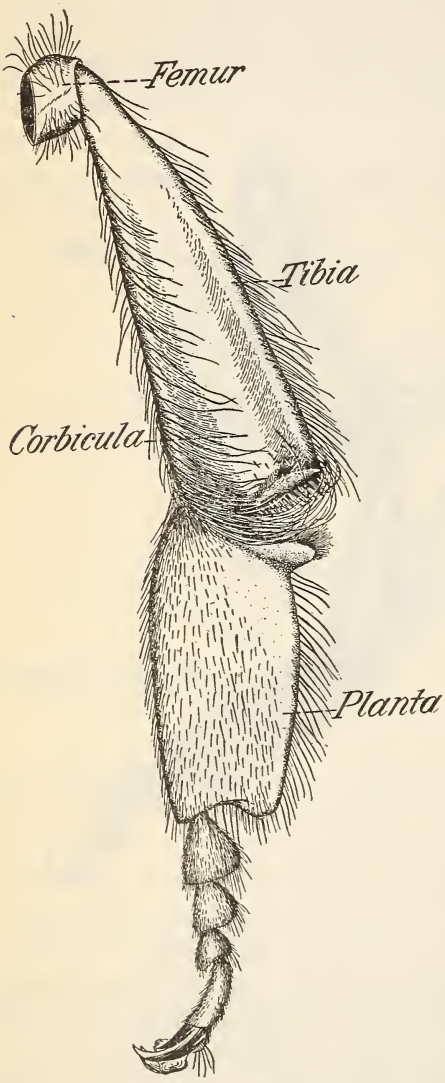

FIG. 3.—Outer surface of the left hind leg of a worker bee. (Original.)

The supply of pollen which is available for the bees varies greatly among different flowers. Some furnish an abundant amount and present it to the bee in such a way that little difficulty is experienced in quickly securing an ample load, while others furnish but little. When flowers are small and when the bee approaches them from above, little, if any, pollen is scattered over the bee's body, all that it acquires being first collected upon the mouth and neighboring parts. Very different conditions are met with when bees visit such plants as corn and ragweed. The flowers of these plants are pendent and possess an abundant supply of pollen, which falls in showers over the bodies of the bees as they crawl beneath the blossoms. The

supply of pollen which lodges upon the body of the bee will thus differ considerably in amount, depending upon the type of flower from which the bee is collecting, and the same is true regarding the location upon the body of a bee of pollen grains which are available for storage in the baskets. Moreover, the movements concerned in the collection of the pollen from the various body parts of the bee upon which it lodges will differ somewhat in the two cases, since a widely scattered supply requires for its collection additional movements, somewhat similar in nature to those which the bee employs in cleaning the hairs which cover its body.

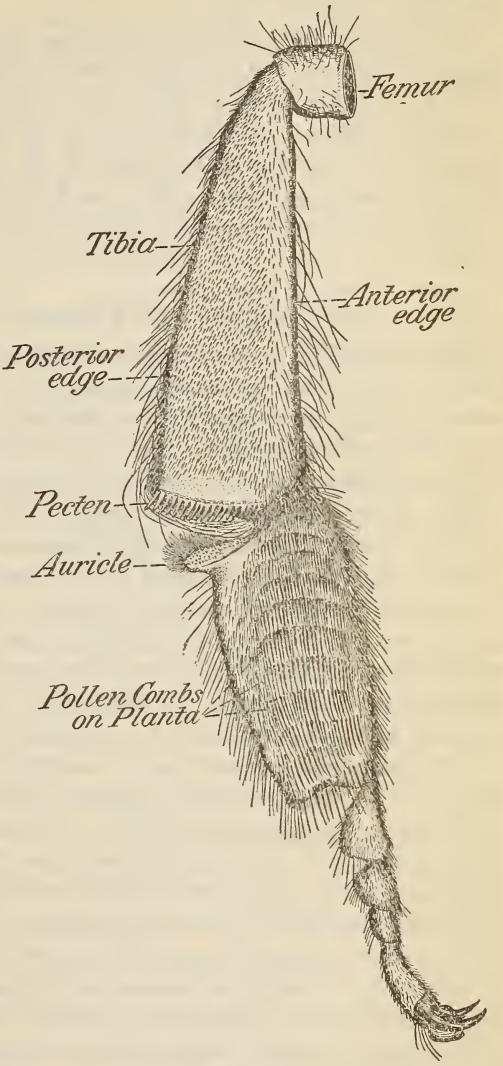

FIG. 4.—Inner surface of the left hind leg of a worker bee. (Original.)

GENERAL STATEMENT OF THE POLLEN-COLLECTING PROCESS.

A very complete knowledge of the pollen-gathering behavior of the worker honey bee may be obtained by a study of the actions of bees which are working upon a plant which yields pollen in abundance. Sweet corn is an ideal plant for this purpose, and it will be used as a basis for the description which follows.

In attempting to outline the method by which pollen is manipulated the writer wishes it to be understood that he is recounting that which he has seen and that the description is not necessarily complete, although he is of the opinion that it is very nearly so. The movements of the legs and of the mouthparts are so rapid and so many

members are in action at once that it is impossible for the eye to follow all at the same time. However, long-continued observation, assisted by the study of instantaneous photographs, gives confidence that the statements recorded are accurate, although some movements may have escaped notice.

To obtain pollen from corn the bee must find a tassel in the right stage of ripeness, with flowers open and stamens hanging from them. The bee alights upon a spike and crawls along it, clinging to the pendent anthers. It crawls over the anthers, going from one flower to another along the spike, being all the while busily engaged in the task of obtaining pollen. This reaches its body in several ways.

As the bee moves over the anthers it uses its mandibles and tongue, biting the anthers and licking them and securing a considerable amount of pollen upon these parts. This pollen becomes moist and sticky, since it is mingled with fluid from the mouth. A considerable amount of pollen is dislodged from the anthers as the bee moves over them. All of the legs receive a supply of this free pollen and much adheres to the hairs which cover the body, more particularly to those upon the ventral surface. This free pollen is dry and powdery and is very different in appearance from the moist pollen masses with which the bee returns to the hive. Before the return journey this pollen must be transferred to the baskets and securely packed in them.

After the bee has traversed a few flowers along the spike and has become well supplied with free pollen it begins to collect it from its body, head, and forward appendages and to transfer it to the posterior pair of legs. This may be accomplished while the bee is resting upon the flower or while it is hovering in the air before seeking additional pollen. It is probably more thoroughly and rapidly accomplished while the bee is in the air, since all of the legs are then free to function in the gathering process.

If the collecting bee is seized with forceps and examined after it has crawled over the stamens of a few flowers of the corn, its legs and the ventral surface of its body are found to be thickly powdered over with pollen. If the bee hovers in the air for a few moments and is then examined very little pollen is found upon the body or upon the legs, except the masses within the pollen baskets. While in the air it has accomplished the work of collecting some of the scattered grains and of storing them in the baskets, while others have been brushed from the body.

In attempting to describe the movements by which this result is accomplished it will be best first to sketch briefly the rôles of the three pairs of legs. They are as follows:

(*a*) The first pair of legs remove scattered pollen from the head and the region of the neck, and the pollen that has been moistened by fluid substances from the mouth.

(*b*) The second pair of legs remove scattered pollen from the thorax, more particularly from the ventral region, and they received the pollen that has been collected by the first pair of legs.

(*c*) The third pair of legs collect a little of the scattered pollen from the abdomen and they receive pollen that has been collected by the second pair. Nearly all of this pollen is collected by the pollen combs of the hind legs, and is transferred from the combs to the pollen baskets or corbiculæ in a manner to be described later.

It will thus be seen that the manipulation of pollen is a successive process, and that most of the pollen at least passes backward from the point where it happens to touch the bee until it finally reaches the corbiculæ or is accidentally dislodged and falls from the rapidly moving limbs.

ACTION OF THE FORELEGS AND MOUTHPARTS.

Although the pollen of some plants appears to be somewhat sticky, it may be stated that as a general rule pollen can not be successfully manipulated and packed in the baskets without the addition of some fluid substance, preferably a fluid which will cause the grains to cohere. This fluid, the nature of which will be considered later, comes from the mouth of the bee, and is added to the pollen which is collected by the mouthparts and to that which is brought into contact with the protruding tongue and maxillæ, and, as will appear, this fluid also becomes more generally distributed upon the legs and upon the ventral surface of the collecting bee.

When a bee is collecting from the flowers of corn the mandibles are actively engaged in seizing, biting, and scraping the anthers as the bee crawls over the pendent stamens. Usually, but not always, the tongue is protruded and wipes over the stamens, collecting pollen and moistening the grains thus secured. Some of the pollen may possibly be taken into the mouth. All of the pollen which comes in contact with the mouthparts is thoroughly moistened, receiving more fluid than is necessary for rendering the grains cohesive. This exceedingly wet pollen is removed from the mouthparts by the forelegs (fig. 5), and probably the middle legs also secure a little of it directly, since they sometimes brush over the lower surface of the face and the mouth. In addition to removing the very moist pollen from the mouth the forelegs also execute cleansing movements over the sides of the head and neck and the anterior region of the thorax, thereby collecting upon their brushes a considerable amount of pollen which has fallen directly upon these regions, and this is added to the pollen moistened from the mouth, thereby becoming moist by contact. The brushes of the forelegs also come in contact with the anterior breast region, and the hairs which cover this area become moist with the sticky exudation which the forelegs have acquired in the process of wiping pollen from the tongue, maxillæ, and mandibles.

ACTION OF THE MIDDLE LEGS.

The middle legs are used to collect the pollen gathered by the forelegs and mouthparts, to remove free pollen from the thoracic region, and to transport their load of pollen to the hind legs, placing most of it upon the pollen combs of these legs, although a slight amount is directly added to the pollen masses in the corbiculæ. Most of the pollen of the middle legs is gathered upon the conspicuous brushes of the first tarsal segments or plantæ of these legs.

In taking pollen from a foreleg the middle leg of the same side is extended in a forward direction and is either grasped by the flexed foreleg or rubbed over the foreleg as it is bent downward and backward. In the former movement the foreleg flexes sharply upon itself until

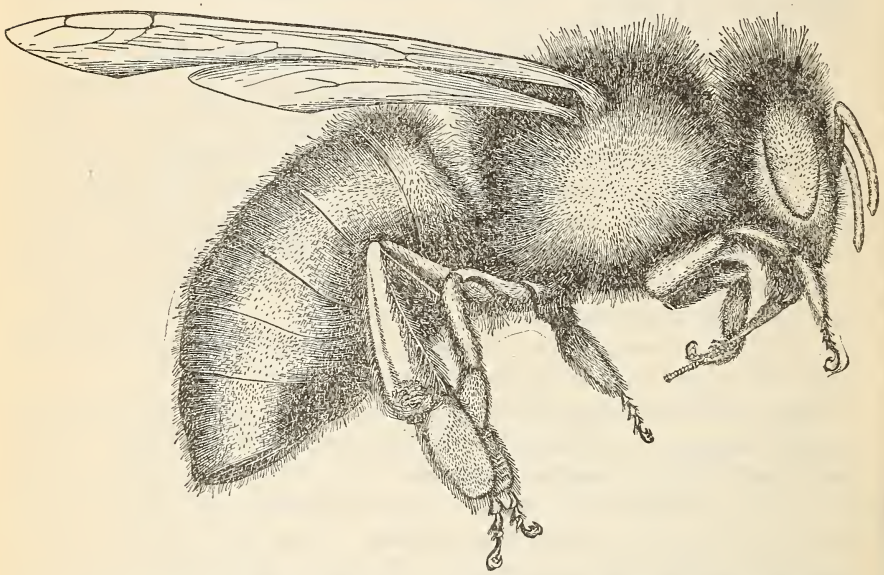

FIG. 5.—A flying bee, showing the manner in which the forelegs and middle legs manipulate pollen. The forelegs are removing wet pollen from the mouthparts and face. The middle leg of the right side is transferring the pollen upon its brush to the pollen combs of the left hind planta. A small amount of pollen has already been placed in the baskets. (Original.)

the tarsal brush and coxa nearly meet. The collecting brush of the middle leg is now thrust in between the tarsus and coxa of the foreleg and wipes off some of the pollen from the foreleg brush. The middle leg brush is then raised and combs down over the flexed foreleg, thus removing additional pollen from the outer surface of this leg. The middle leg also at times reaches far forward, stroking down over the foreleg before it is entirely flexed and apparently combing over with its tarsal brush the face and mouthparts themselves. When the middle leg reaches forward to execute any of the above movements the direction of the stroke is outward, forward, and then back toward the body, the action ending with the brush of the leg in contact with the long hairs of the breast and with those which spring

from the proximal segments of the forelegs (coxa, trochanter, femur). As a result of the oft-repeated contact of the brushes of the middle and forelegs with the breast, the long, branched hairs which cover this region become quite moist and sticky, since the brushes of these two pair of legs are wet and the pollen which they bear possesses a superabundance of the moistening fluid. Any dry pollen which passes over this region and touches these hairs receives moisture by contact with them. This is particularly true of the free dry pollen which the middle pair of legs collect by combing over the sides of the thorax.

The pollen upon the middle legs is transferred to the hind legs in at least two ways. By far the larger amount is deposited upon the pollen combs which lie on the inner surfaces of the plantæ of the

FIG. 6.—A bee upon the wing, showing the position of the middle legs when they touch and pat down the pollen masses. A very slight amount of pollen reaches the corbiculæ through this movement. (Original.)

hind legs. To accomplish this a middle leg is placed between the plantæ of the two hind legs, which are brought together so as to grasp the brush of the middle leg, pressing it closely between them, but allowing it to be drawn toward the body between the pollen combs of the two hind legs. (See fig. 5.) This action results in the transference of the pollen from the middle-leg brush to the pollen combs of the hind leg of the opposite side, since the combs of that leg scrape over the pollen-laden brush of the middle leg. This action may take place while the bee is on the wing or before it leaves the flower.

The middle legs place a relatively small amount of pollen directly upon the pollen masses in the corbiculæ. This is accomplished when the brushes of the middle legs are used to pat down the pollen masses and to render them more compact. (See fig. 6.) The legs are used

for this purpose quite often during the process of loading the baskets, and a small amount of pollen is incidentally added to the masses when the brushes come into contact with them. A misinterpretation of this action has led some observers into the erroneous belief that all or nearly all of the corbicular pollen is scraped from the middle-leg brushes by the hairs which fringe the sides of the baskets. The middle legs do not scrape across the baskets, but merely pat downward upon the pollen which is there accumulating.

It is also possible that, in transferring pollen from the middle leg of one side to the planta of the opposite hind leg, the middle-leg brush may touch and rub over the pecten of the hind leg and thus directly place some of its pollen behind the pecten spines. Such a result is, however, very doubtful.

ACTION OF THE HIND LEGS.

The middle legs contribute the major portion of the pollen which reaches the hind legs, and all of it in cases where all of the pollen first reaches the bee in the region of the mouth. However, when much pollen falls upon the body of the bee the hind legs collect a little of it directly, for it falls upon their brushes and is collected upon them when these legs execute cleansing movements to remove it from the ventral surface and sides of the abdomen. All of the pollen which reaches the corbiculæ, with the exception of the small amount placed there by the middle legs when they pat down the pollen masses, passes first to the pollen combs of the plantæ.

When in the act of loading pollen from the plantar brushes to the corbiculæ the two hind legs hang beneath the abdomen with the tibiofemoral joints well drawn up toward the body. (See fig. 7.) The two plantæ lie close together with their inner surfaces nearly parallel to each other, but not quite, since they diverge slightly at their distal ends. The pollen combs of one leg are in contact with the pecten comb of the opposite leg. If pollen is to be transferred from the right planta to the left basket, the right planta is drawn upward in such a manner that the pollen combs of the right leg scrape over the pecten spines of the left. By this action some of the pollen is removed from the right plantar combs and is caught upon the outer surfaces of the pecten spines of the left leg.

This pollen now lies against the pecten and upon the flattened distal end of the left tibia. At this moment the planta of the left leg is flexed slightly, thus elevating the auricle and bringing the auricular surface into contact with the pollen which the pecten has just received. By this action the pollen is squeezed between the end of the tibia and the surface of the auricle and is forced upward against the distal end of the tibia and on outward into contact with the pollen mass accumulating in the corbicula. As this act, by which the left

basket receives a small contribution of pollen, is being completed, the right leg is lowered and the pecten of this leg is brought into contact with the pollen combs of the left planta, over which they scrape as the left leg is raised, thus depositing pollen upon the lateral surfaces of the pecten spines of the right leg. (See fig. 7.)

Right and left baskets thus receive alternately successive contributions of pollen from the planta of the opposite leg. These loading movements are executed with great rapidity, the legs rising and falling with a pump-like motion. A very small amount of pollen is loaded at each stroke and many strokes are required to load the baskets completely.

If one attempts to obtain, from the literature of apiculture and zoology, a knowledge of the method by which the pollen baskets

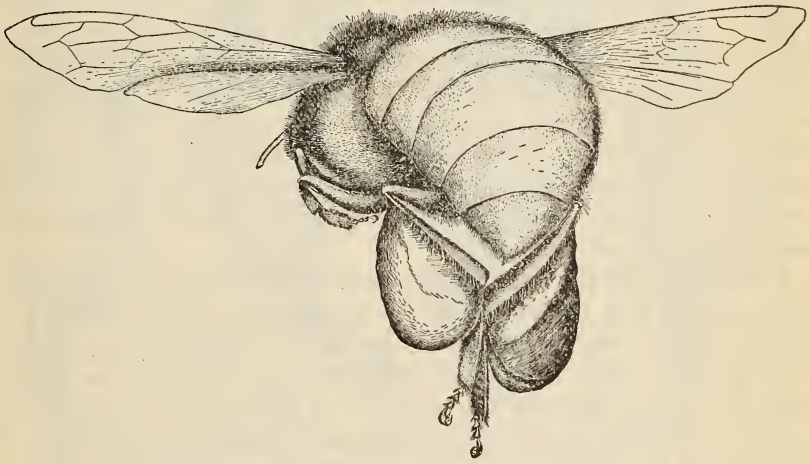

FIG. 7.—A bee upon the wing, showing the manner in which the hind legs are held during the basket-loading process. Pollen is being scraped by the pecten spines of the right leg from the pollen combs of the left hind planta. (Original.)

themselves are loaded, he is immediately confused by the diversity of the accounts available. The average textbook of zoology follows closely Cheshire's (1886) description in which he says that "the legs are crossed, and the metatarsus naturally scrapes its comb face on the upper edge of the opposite tibia in the direction from the base of the combs toward their tips. These upper hairs * * * are nearly straight, and pass between the comb teeth. The pollen, as removed, is caught by the bent-over hairs, and secured. Each scrape adds to the mass, until the face of the joint is more than covered, and the hairs just embrace the pellet." Franz (1906) states that (translated) "the final loading of the baskets is accomplished by the crossing over of the hind-tarsal segments, which rub and press upon each other." Many other observers and textbook writers evidently believed that the hind legs were crossed in the loading process.

On the other hand, it is believed by some that the middle legs are directly instrumental in filling the baskets. This method is indicated in the following quotation from Fleischmann and Zander (1910) (translated):

> The second pair of legs transfer the pollen to the hind legs, where it is heaped up in the pollen masses. The tibia of each hind leg is depressed on its outer side, and upon the edges of this depression stand two rows of stiff hairs which are bent over the groove. The brushes of the middle pair of legs rub over these hairs, liberating the pollen, which drops into the baskets.

A suggestion of the true method is given by Hommell (1906), though his statements are somewhat indefinite. After describing the method by which pollen is collected, moistened, and passed to the middle legs he states that (translated) "the middle legs place their loads upon the pollen combs of the hind legs. There the sticky pollen is kneaded and is pushed across the pincher (*à traverse la pince*), is broken up into little masses and accumulates within the corbicula. In accomplishing this, the legs cross and it is the tarsus of the right leg which pushes the pollen across the pincher of the left, and reciprocally. The middle legs never function directly in loading the baskets, though from time to time their sensitive extremities touch the accumulated mass, for the sake of giving assurance of its position and size."

The recent valuable papers of Sladen (1911, 1912, *a*, *b*, *c*, *d*, and *e*), who was the first to present a true explanation of the function of the abdominal scent gland of the bee, give accounts of the process by which the pollen baskets are charged, which are in close accord with the writer's ideas on this subject. It is a pleasure to be able to confirm most of Sladen's observations and conclusions. and weight is added to the probable correctness of the two descriptions and interpretations of this process by the fact that the writer's studies and the conclusion based upon them were made prior to the appearance of Sladen's papers and quite independent of them. His description of the basket-loading process itself is so similar to the writer's own that a complete quotation from him is unnecessary. A few differences of opinion will, however, be noted while discussing some of the movements which the process involves. As will later be noted, our ideas regarding the question of pollen moistening, collecting, and transference are somewhat different.

ADDITIONAL DETAILS OF THE BASKET-LOADING PROCESS.

The point at which pollen enters the basket can best be determined by examining the corbiculæ of a bee shortly after it has reached a flower and before much pollen has been collected. Within each pollen basket of such a bee is found a small mass of pollen, which lies

along the lower or distal margin of the basket. (See fig 8, *a*.) It is in this position because it has been scraped from the planta of the opposite leg by the pecten comb and has been pushed upward past the entrance of the basket by the continued addition of more from below, propelled by the successive strokes of the auricle. Closer

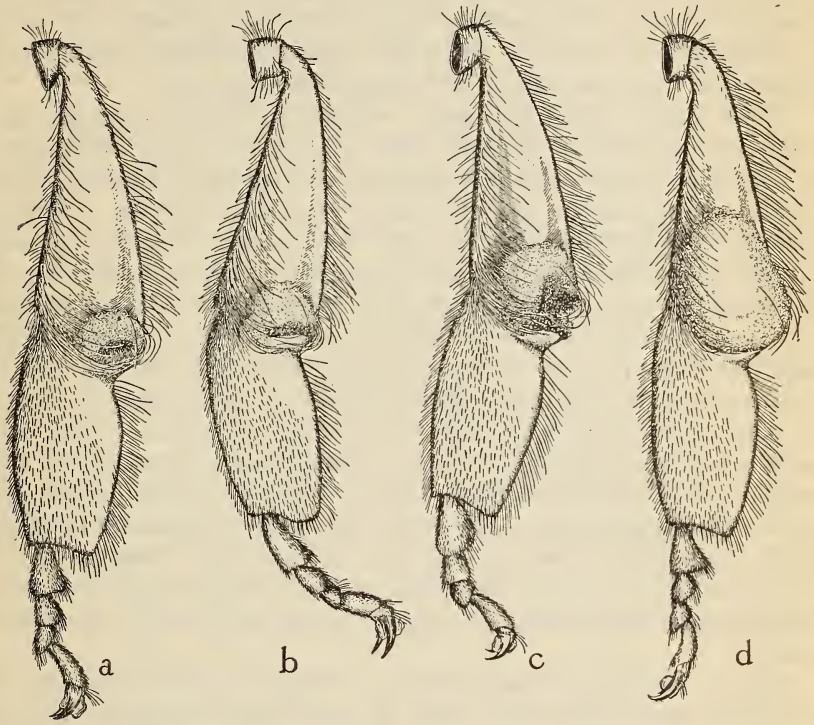

FIG. 8.—Camera drawings of the left hind legs of worker bees to show the manner in which pollen enters the basket. *a*, Shows a leg taken from a bee which is just beginning to collect. It had crawled over a few flowers and had flown in the air about five seconds at the time of capture. The pollen mass lies at the entrance of the basket, covering over the fine hairs which lie along this margin and the seven or eight short stiff spines which spring from the floor of the corbicula immediately above its lower edge. As yet the pollen has not come in contact with the one long hair which rises from the floor and arches over the entrance. The planta is extended, thus lowering the auricle; *b*, represents a slightly later stage, showing the increase of pollen. The planta is flexed, raising the auricle. The hairs which extend outward and upward from the lateral edge of the auricle press upon the lower and outer surface of the small pollen mass, retaining it and guiding it upward into the basket; *c*, *d*, represent slightly later stages in the successive processes by which additional pollen enters the basket. (Original.)

examination of the region between the pecten and the floor of the basket itself shows more pollen, which is on its way to join that already squeezed into the basket.

If the collecting bee is watched for a few moments the increase will readily be noted and the fact will be established that the accumulating mass is gradually working upward or proximally from the lower

or distal edge of the corbicula and is slowly covering the floor of this receptacle. (See fig. 8, *b*, *c*, and *d*.) In many instances the successive contributions remain for a time fairly separate, the whole mass being marked by furrows transverse to the long axis of the tibia.

Sladen (1912, *b*) notes the interesting fact that in those rather exceptional cases when a bee gathers pollen from more than one species of flowers the resulting mass within the corbicula will show a stratification parallel to the distal end, a condition which could result only from the method of loading here indicated.

As the pollen within the basket increases in amount it bulges outward, and projects downward below the lower edge of the basket. It is held in position by the long hairs which fringe the lateral sides of the basket, and its shape is largely determined by the form of these hairs and the direction in which they extend. When the basket is fully loaded the mass of pollen extends laterally on both sides of the tibia, but projects much farther on the posterior side, for on this side the bounding row of hairs extends outward, while on the anterior edge the hairs are more curved, folding upward and over the basket. As the mass increases in thickness by additions from below it is held in position by these long hairs which edge the basket. They are pushed outward and many of them become partly embedded in the pollen as it is pushed up from below. When the pollen grains are small and the whole mass is well moistened the marks made by some of the hairs will be seen on the sides of the load. (See fig. 9, *a*.) These scratches are also transverse in direction and they show that the mass has been increased by additions of pollen pushed up from below.

Even a superficial examination of a heavily laden basket shows the fallacy of the supposition that the long lateral fringing hairs are used to comb out the pollen from the brushes of either the hind or middle legs by the crossing of these legs over the lateral edges of the baskets. They are far from sufficiently stiff to serve this purpose, and their position with relation to the completed load shows conclusively that they could not be used in the final stages of the loading process, for the pollen mass has completely covered many of them and its outer surface extends far beyond their ends. They serve merely to hold the pollen in place and to allow the load to project beyond the margins of the tibia.

The auricle plays a very essential part in the process of loading the basket. This structure comprises the whole of the flattened proximal surface of the planta, except the joint of articulation itself, and it extends outward in a posterior direction a little beyond the remaining plantar edge. The surface of the auricle is covered over with many blunt, short spines and its lateral margin is bounded by a row of short rather pliable hairs, branched at their ends. When

the planta is flexed the auricle is raised and its surface approaches the distal end of the tibia, its inner edge slipping up along the pecten spines and its outer hairy edge projecting into the opening which leads to the pollen basket. (See fig. 8, *b*.) With each upward stroke of the auricle small masses of pollen which have been scraped from the plantar combs by the pecten are caught and compressed between the spiny surface of the auricle and the surface of the tibia above it. The pressure thus exerted forces the pasty pollen outward and upward, since it can not escape past the base of the pecten, and directs it into the entrance to the corbicula. The outward and upward slant of the auricular surface and the projecting hairs with which the outer edge of the auricle is supplied also aid in directing the pollen toward the basket. Sladen (1911) states that in this movement the weak wing of the auricle is forced backward, and thus allows the escape of pollen toward the basket entrance, but this appears both doubtful and unnecessary, since the angle of inclination of the auricular surface gives the pollen a natural outlet in the proper direction.

If the corbicula already contains a considerable amount of pollen the contributions which are added to it at each stroke of the auricle come in contact with that already deposited and form a part of this mass, which increases in amount by continued additions from below. If, however, the corbicula is empty and the process of loading is just beginning, the first small bits of pollen which enter the basket must be retained upon the floor of the chamber until a sufficient amount has accumulated to allow the long overcurving hairs to offer it effective support. The sticky consistency of the pollen renders it likely to retain contact with the basket, and certain structures near the entrance give additional support. Several small sharp spines, seven or eight in number, spring from the floor of the basket immediately within the entrance, and the entire lower edge of the corbicula is fringed with very small hairs which are branched at their ends. (See fig. 3.) One large hair also springs from the floor of the basket, somewhat back from the entrance, which may aid in holding the pollen, but it can not function in this manner until a considerable amount has been collected.

As the pollen mass increases in size and hangs downward and backward over the pecten and auricle it shows upon its inner and lower surface a deep groove which runs outward from the entrance to the basket. (See fig. 9, *b*.) This groove results from the continued impact of the outer end of the auricle upon the pollen mass. At each upward stroke of the auricle its outer point comes in contact with the stored pollen as soon as the mass begins to bulge backward from the basket.

Although the process is a rather delicate one, it is entirely possible so to manipulate the hind legs of a recently killed bee that the

corbiculæ of the two legs receive loads of pollen in a manner similar to that above described. To accomplish this successfully the operator must keep the combs of the plantæ well supplied with moistened pollen. If the foot of first one leg and then the other is grasped with forceps and so guided that the pollen combs of one leg rasp over the pecten spines of the other, the pollen from the combs will be transferred to the corbiculæ. To continue the loading process in a proper manner, it is also necessary to flex the planta of each leg just after the pollen combs of the opposite leg have deposited pollen behind the pecten. By this action the auricle is raised, compressing the pollen which the pecten has secured, and forcing some upward into the corbicula. Bees' legs which have been loaded in this artificial manner show pollen masses in their corbiculæ which are entirely similar in appearance to those formed by the labors of the living bee. Moreover, by the above method of manipulation the pollen appears first at the bottom of the basket, along its lower margin, gradually extends upward along the floor of the chamber, comes in contact with the overhanging hairs, and is shaped by them in a natural manner. All attempts to load the baskets by other movements, such as crossing the hind legs and scraping the plantar combs over the lateral edges of the baskets, give results which are entirely different from those achieved by the living bee.

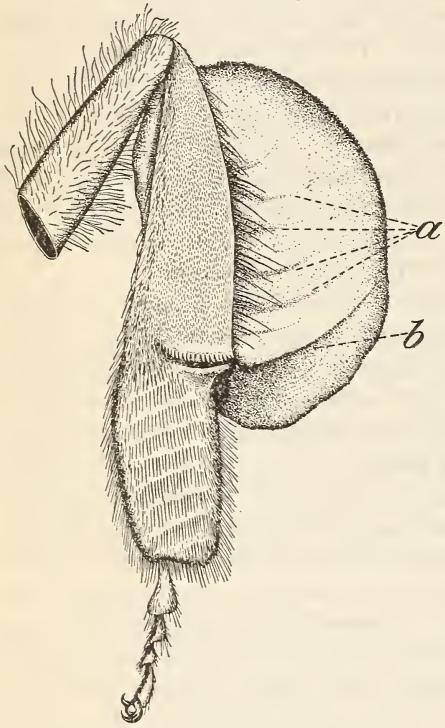

FIG. 9.—Inner surface of the right hind leg of a worker bee which bears a complete load of pollen. *a*, Scratches in the pollen mass caused by the pressure of the long projecting hairs of the basket upon the pollen mass as it has been pushed up from below; *b*, groove in the pollen mass made by the strokes of the auricle as the mass projects outward and backward from the basket. (Original.)

POLLEN MOISTENING.

Many descriptions have been written by others of the method by which pollen is gathered and moistened. Some of these are indefinite, some are incorrect, while others are, in part, at least, similar

to my own interpretation of this process. A few citations will here be given:

The bee first strokes the head and the proboscis with the brushes of the forelegs and moistens these brushes with a little honey from the proboscis, so that with later strokes all of the pollen from the head is collected upon these brushes. Then the middle-leg brushes remove this honey-moistened pollen from the forelegs and they also collect pollen from the breast and the sides of the thorax.—[Translation from Alefeld, 1861.]

In his account of the basket-loading process Alefeld assigns to the middle-leg brushes the function of assembling all of the pollen, even that from the plantar combs, and of placing it on the corbiculæ, this latter act being accomplished by combing over the hairy edge of each basket with the middle-leg brush of the same side.

It appears probable that the bee removes the pollen from the head, breast, and abdomen by means of the hairy brushes which are located upon the medial sides of the tarsal segments of all of the legs, being most pronounced upon the hind legs. The pollen is thus brought together and is carried forward to the mouth, where it is moistened with saliva and a little honey.—[Translation from Franz, 1906.]

Franz then says that this moistened pollen is passed backward and loaded.

Since the pollen of many plants is sticky and moist it adheres to the surface of the basket. Dry pollen is moistened by saliva, so that it also sticks.—[Translation from Fleischmann and Zander, 1910.]

Pollen is taken from flowers principally by means of the tongue, but at times, also, by the mandibles, by the forelegs, and middle legs. The brushes of the hind legs also load themselves, collecting from the hairs of the body. The pollen dust thus gathered is always transmitted to the mouth, where it is mixed with saliva.—[Translation from Hommell, 1906.]

Sladen considers the question of how pollen is moistened by the honey bee, humblebee (bumblebee), and some other bees, but does not appear to reach definite conclusions. In one of his papers (1912, *c*) he states that the pollen of some plants may be found in the mouth cavity and in the region of the mouth, but he reaches the conclusion that this pollen is comparatively "dry," using the word in a "relative sense." He asserts that "nowhere but on the corbicula and hind metatarsal brushes did I find the sticky pollen, except sometimes on the tips of the long, branched hairs on the back (upper) edges of the tibiæ and femora of the middle legs, and then only in heavily laden bees, where it is reasonable to suppose it had collected accidentally as the result of contact with the hind metatarsal brushes."

These and other considerations lead Sladen to think that, in the case of the bumblebee at least, the pollen "may be moistened on the hind metatarsus with the tongue." He states that the tongue of the bumblebee is of sufficient length to reach the hind metatarsus

(planta) and that it might rub over the brushes of the metatarsi or be caught between them when they are approximated and thus moisten the two brushes simultaneously. However, he has never seen the tongue of the collecting honey bee brought near to the hind legs, and it appears probable to him that it can not easily reach them. "Possibly the middle or front legs are used as agents for conveying the honey" (in the case of the honey bee). "In the humblebee the tongue is longer, and it could more easily moisten the hind legs in the way suggested."

In an earlier paper Sladen (1912, *a*) gives the following as his opinion of the "way in which pollen dust is moistened with nectar," although he states that this is one of the points "which still remains obscure":

> The only satisfactory manner in which, it seems to me, this can be done is for the tongue to lick the tarsi or metatarsi of the forelegs, which are covered with stiff bristles, well suited for holding the nectar, the nectar being then transferred to the metatarsal brushes on the middle legs, and from these, again, to the metatarsal brushes on the hind legs. The latter being thus rendered sticky, the pollen dust would cling to them. The different pairs of legs were certainly brought together occasionally, but not after every scrape of the hind metatarsi, and their movements were so quick that it was impossible to see what was done. Still, several pollen-collecting bees that I killed had the tarsi and metatarsi of the forelegs and the metatarsal brushes of the middle and hind legs moistened with nectar, and I think it probable that the moistening process, as outlined, is performed, as a rule, during the flight from flower to flower.

Sladen (1912, *c*) also considers the possibility that the fluid which moistens the pollen might be secreted through the comb at the end of the tibia, through the tibio-tarsal joint, or from the surface of the auricle, but finds no evidence of glandular openings in these regions. A suggestion of a similar nature, apparently unknown to Sladen, was made by Wolff (1873), who describes "sweat-glands" which, he claims, are located within the hind tibia and the planta, and which pour a secretion upon the surface of the corbicula and upon the upper end of the planta through many minute openings located at the bases of hairs, particularly those which arise from the lateral margins of the corbicula. Wolff is convinced that the fluid thus secreted is the essential cohesive material by which the grains of pollen are bound together to form the solid mass which fills each fully loaded basket. He noticed that the mouthparts are used to collect pollen, and that some of it is moistened with "honey" or "nectar," but he does not consider that the fluid thus supplied is sufficient to explain adequately the facility with which the collecting bee brings together the scattered grains of pollen and packs them away securely in the baskets. Wolff's description of the basket-loading process itself is strikingly similar to that advocated later by Cheshire.

The writer is not prepared to deny the possibility that the surface of the chitin of the hind legs of worker bees may be moistened by the secretion of glands which lie beneath it, but he is convinced that any fluid thus secreted bears little or no relation to the cohesion of the pollen grains within the baskets. Sections and dissected preparations of the hind legs of worker bees show certain large cells which lie within the cavity of the leg and which may function as secreting gland cells; but similar structures occur in even greater numbers within the hind legs of the drone and they are found within the hind legs of the queen.

As has been noted, the extreme moisture of the plantar combs and of the tibio-tarsal articulation of the hind leg is readily understood when one recalls the manner in which moist pollen is compressed between the auricle and the tibial surface above it.

From the account already given it is evident that, in the opinion of the writer, the mouth is the source from which the pollen-moistening fluid is obtained. It is extremely difficult to determine with absolute accuracy the essential steps involved in the process of adding moisture to the pollen. In an endeavor to solve this problem the observer must of necessity consider a number of factors, among which may be noted (1) the location upon the body of the collecting bee of "moist" and of comparatively "dry" pollen, (2) the movements concerned in the pollen-gathering and pollen-transferring processes, (3) the relative moisture of those parts which handle pollen, (4) the chemical differences between the natural pollen of the flower and that of the corbiculæ and of the cells of the hive, and (5) the observer must endeavor to distinguish between essential phenomena and those which are merely incidental or accidental.

In the first place it should be noted that the relative dampness of pollen within the corbiculæ depends very largely upon the character of the flower from which the pollen grains are gathered. When little pollen is obtained it is much more thoroughly moistened, and this is particularly true in cases when the pollen is all, or nearly all, collected in the region of the mouth, the forelegs, and head. When a bee takes pollen from white or sweet clover practically all of it first touches the bee in these regions. It immediately becomes moist, and in this condition is passed backward until it rests within the baskets. There is here no question of "dry" and "wet" pollen, or of collecting movements to secure dry pollen from other regions of the body, or of the ultimate method by which such free, dry pollen becomes moist.

The sticky fluid which causes pollen grains to cohere is found upon all of the legs, in the region of their brushes, although the pollen combs and auricles of the hind legs are likely to show it in greatest abundance, since nearly all of the pollen within each basket has

passed over the auricle, has been pressed upward and squeezed between the auricle and the end of the tibia and the pollen mass above, and by this compression has lost some of its fluid, which runs down over the auricle and onto the combs of the planta. It is not necessary to invoke any special method by which these areas receive their moisture. The compressing action of the auricle squeezing heavily moistened pollen upward into the basket is entirely sufficient to account for the abundance of sticky fluid found in the neighborhood of each hind tibio-tarsal joint. As has been noted, the brushes of the forelegs acquire moisture directly by stroking over the proboscis and by handling extremely moist pollen taken from the mouthparts. The middle-leg brushes become moist by contact with the foreleg and hind-leg brushes, probably also by touching the mouthparts themselves, and by passing moist pollen backward. The hairy surface of the breast is moistened by contact with the fore and mid leg brushes and with the moist pollen which they bear.

The problem of the method of pollen moistening is somewhat more complicated in the case of flowers which furnish an excessive supply. Under such conditions the entire ventral surface of the collecting bee becomes liberally sprinkled with pollen grains which either will be removed and dropped or will be combed from the bristles and branching hairs, kneaded into masses, transferred, and loaded. The question naturally arises whether the movements here are the same as when the plant yields but a small amount of pollen which is collected by the mouthparts and anterior legs. In the opinion of the writer they are essentially the same, except for the addition of cleansing movements, executed chiefly by the middle and hind legs for the collection of pollen which has fallen upon the thorax, upon the abdomen, and upon the legs themselves. Indeed it is questionable as to just how much of this plentiful supply of free pollen is really used in forming the corbicular masses. Without doubt much of it falls from the bee and is lost, and in cases where it is extremely abundant and the grains are very small in size an appreciable amount still remains entangled among the body-hairs when the bee returns to the hive. Yet it is also evident that some of the dry pollen is mingled with the moistened material which the mouthparts and forelegs acquire and together with this is transferred to the baskets.

In all cases the pollen-gathering process starts with moist pollen from the mouth region. This pollen is passed backward, and in its passage it imparts additional moisture to those body regions which it touches, the brushes of the fore and middle legs, the plantæ of the hind legs, and the hairs of the breast which are scraped over by the fore and middle leg brushes. This moist pollen, in its passage backward, may also pick up and add to itself grains of dry pollen with which it accidentally comes in contact. Some of the free, dry pollen

which falls upon the moist brushes or upon the wet hairs of the thorax is also dampened. Some of the dry pollen which is cleaned from the body by the action of all of the legs meets with the wet brushes or with the little masses of wet pollen and itself becomes wet by contact. Pollen grains which reach the corbiculæ either dry or but slightly moistened are soon rendered moist by contact with those already deposited. Little pollen gets by the sticky surfaces of the combs of the plantæ or past the auricles without becoming thoroughly moist.

Sladen (1912, *c*) very aptly compares the mixture of dry pollen with wet to the kneading of wet dough with dry flour and suggests that the addition of dry pollen may be of considerable advantage, since otherwise the brushes, particularly those of the hind legs, would become sticky, "just as the board and rolling pin get sticky in working up a ball of dough if one does not add flour." The addition of a considerable amount of dry pollen gives exactly this result, for the corbiculæ then rapidly become loaded with pollen mixed with a minimum supply of moisture and the brushes remain much dryer than would otherwise be the case. However, if too much dry pollen is added the resulting loads which the bees carry back to the hives are likely to be irregular, for the projecting edges of the masses may crumble through lack of a sufficient amount of the cohesive material by which the grains are bound together.

On the other hand, it does not appear at all necessary to mix much dry pollen with the wet, nor do the brushes become sufficiently "sticky" from the presence of an abundance of the moistening fluid to endanger their normal functional activity. I have observed bees bringing in pollen masses which were fairly liquid with moisture, and the pollen combs also were covered with fluid, yet the baskets were fully and symmetrically loaded.

Sladen's different interpretations of the pollen-moistening process are rather confusing, and it is difficult to distinguish between what he states as observed facts and what he puts forward as likely hypotheses. He agrees with me in his observation that all of the legs become moist in the region of their brushes and also in his supposition that this moisture is transferred to them from the mouth. In this moistening process my observations show that the fluid concerned is passed backward by the contact of the middle-leg brushes with the wet foreleg brushes and that the middle-leg brushes in turn convey moisture to the plantæ as they rub upon them. I am also convinced that the wet pollen grains furnish additional moisture to the brushes as they pass backward, and this is particularly true in the case of the extremely moist surfaces of the auricles and the pollen combs of the planta, since here moisture is pressed from the pollen upon these areas. The pollen upon the fore and middle leg brushes is not always "dry" even in "a relative sense."

In describing pollen manipulation several writers state that dry pollen is picked up by the brushes of the legs and is carried forward to the mouth, there moistened (according to some, masticated), and is then carried backward by the middle legs for loading. Obviously such accounts do not apply to cases in which all of the pollen is collected by mouthparts and forelegs. Do they apply in cases where much pollen falls on the body and limbs? Without doubt a certain amount of this free pollen is brought forward when the middle legs, bearing some of it, sweep forward and downward over the forelegs, mouthparts, and breast. However, it does not appear to the writer that this dry pollen is carried to the mouth for the specific purpose of moistening it, or that it is essential to its moistening that it be brought in contact with the mouth. Some of it touches the moist hairs on the forelegs and breast and is moistened by contact. All that remains on the brushes of the middle legs secures moisture from these brushes or from wet pollen which the brushes collect from the mouthparts or forelegs. The supposed necessity of carrying forward pollen to the mouth for moistening is a delusion. Some is accidentally brought forward and into contact with the mouth and gets wet, but the process is not essential.

If the pollen which bees transport to their hives has been moistened with some fluid substance which causes the grains to cohere, this addition should be indicated by differences in the results of an analysis of pollen from a plant as compared with that found in the corbiculæ of a bee which has been working on this plant. For the sake of determining this difference and in an endeavor to ascertain, if possible, the approximate nature of the added fluid, analyses were made of three kinds of pollen, as follows: (1) Pollen collected by hand from the corn plant itself; (2) pollen taken from the corbiculæ of bees which had secured their supply from corn; (3) pollen stored in the cells of the hive. In the first two cases pollen from the same species of plant (corn) was used. The material from the cells of the hive was composed largely of corn pollen, but contained an admixture of some other pollens.

The writer is indebted to Dr. P. B. Dunbar, of the Bureau of Chemistry, for the following analyses:

	Pollen direct from corn.	Corn pollen from corbicula.	Stored pollen from hive.
Total solids	53.47	66.94	79.66
Moisture	46.53	33.06	20.34
Reducing sugar before inversion	2.87	11.07	17.90
Sucrose	2.77	3.06	2.25
Total reducing sugar after inversion	5.79	14.29	20.27
Dry basis:			
Reducing sugar	5.37	16.54	22.47
Sucrose	5.18	4.57	2.82
	10.55	21.11	.....

These analyses show conclusively that a very large amount of sugar has been added to the pollen by the time it reaches the corbiculæ. Calculated on a dry basis just about twice as much sugar is present in the basket pollen as in that from the corn plant. Not only is this so, but the additional fact is disclosed that over three times as much reducing sugar is present in the corbicular pollen as sucrose. This latter result indicates that honey (largely a reducing sugar) rather than nectar (containing more sucrose) is the chief sugar ingredient of the corbicular pollen. The additional amount of sugar (here again a reducing sugar) in the stored pollen of the hive is what might be expected, since it is supposed that the workers add honey and possibly other ingredients to the pollen within the storage cells.

The total solid percentages, corn 53.47, corbicula 66.94, stored pollen 79.66, also show that the fluid substance which is added is one highly charged with solids, a condition which honey amply fulfills.

In the descriptions which have been cited of the pollen-gathering process in which the mouth is supposed to supply the requisite fluid three substances are mentioned: Nectar, honey, and saliva. The analyses herein given indicate that reducing sugar is mingled with the pollen, and in the case of corn it is indicated that honey is used in greater abundance. Without doubt a certain amount of saliva also finds its way to the pollen, but the proportion of this substance has not been determined. This salivary fluid may have adhesive qualities, but this is scarcely necessary, since honey alone is amply sufficient for this purpose.

It appears probable that the fluid which a bee adds to the pollen which it is collecting varies somewhat in amount, since the pollen of different plants differs considerably in moisture content and that of the same plant will differ in this respect at different times. Pollen collected in the early morning before the dew has left the plant is much more moist than that found upon the same plant later in the day, and the grains, if taken when moist, have a natural tendency to become aggregated and form small masses. Moreover, this may explain the fact that bees make their pollen-collecting trips during the morning hours, rather than in the afternoon, although some may be seen upon the flowers throughout the whole day.

STORING POLLEN IN THE HIVE.

When the bee has fully loaded its baskets and before it returns to the hive it often spends a little time upon the plant from which it has been collecting, occupied with the task of cleaning scattered grains of pollen from its body and of patting down securely the loads which it has obtained. Upon its return to the hive it hurries within and seeks for a suitable place in which to deposit the pollen. Some

returning bees walk leisurely over the combs and loiter among their sister workers, while others appear to be greatly agitated, shaking their bodies and moving their wings as though highly excited. Many pollen-bearing bees appear eager to receive food upon their return to the hive, and they will solicit it from other workers or take it from the honey-storage cells. The workers of the hive at times take a little of the fresh pollen from the baskets of the laden bee, nibbling it off with their mandibles or rasping off grains with their tongues.

If the combs of a colony are examined, stored pollen will be found in various parts of the hive. In the brood frames the greatest amount is located above and at the sides of the brood and between this and the stored honey. Cells scattered through the brood from which young bees have lately emerged may also contain pollen. In the outer frames of the hive, where brood is less likely to be found, nearly all of the cells may be packed with pollen, or honey-storage cells may be found interspersed with those filled with pollen. As a rule pollen is not stored in drone comb, although this occasionally happens.

As the pollen-bearing bee crawls over the combs it appears to be searching for a suitable cell in which to leave its load. It sticks the head into cell after cell until finally one is located which meets its requirements, although it is an open question as to why any one of a group should be chosen rather than another. This selected cell may already contain some pollen or it may be empty. If partly filled, the pollen which it contains is likely to be from the same species of plant as that which the bee carries, although different kinds of pollen are often stored in the same cell.

In preparation for the act of unloading the bee grasps one edge of the cell with its forelegs and arches its abdomen so that the posterior end of the abdomen rests upon the opposite side of the cell. The body is thus held firmly and is braced by these two supports with the head and anterior thoracic region projecting over one of the neighboring cells. The hind legs are thrust down into the cell and hang freely within it, the pollen masses being held on a level with the outer edge of the cell, or slightly above it. The middle leg of each side is raised and its planta is brought into contact with the upper (proximal) end of the tibia of the same side and with the pollen mass. The middle leg now presses downward upon the pollen mass, working in between it and the corbicular surface, so that the mass is shoved outward and downward and falls into the cell. As the pollen masses drop, the middle legs are raised and their claws find support upon the edge of the cell. The hind legs now execute cleansing movements to remove small bits of pollen which still cling to the corbicular

surfaces and hairs. After this is accomplished the bee usually leaves the cell without paying further attention to the two pellets of pollen although some collecting bees will stick the head into the cell, possibly to assure themselves that the pollen is properly deposited. It has been stated by some (Cheshire, for example) that the spur upon the middle leg is used to help pry the pollen mass from the corbicula. This structure is in close proximity with the mass while the middle leg is pushing downward upon it, but its small size renders difficult an exact estimate of its value in this connection. It is certainly true that the entire planta of the middle leg is thrust beneath the upper end of the pollen mass, but the spur may be used as an entering wedge.

Pollen masses which have been dropped by the collecting bee may remain for some time within the cell without further treatment, but usually another worker attends to the packing of the pollen shortly after it has been deposited. To accomplish this the worker enters the cell head first, seizes the pollen pellets with its mandibles, breaks them up somewhat or flattens them out, probably mingles additional fluid with the pollen, and tamps down the mass securely in the bottom of the cell. As is shown by the analyses of corbicular pollen and of stored pollen, certain substances are added to the pollen after the collecting bee leaves it in the cell. Sugar is certainly added, and it is generally supposed that secretions from some of the salivary glands are mixed with the pollen after deposition. It appears probable that the stored pollen or "beebread" is changed somewhat in chemical composition through the action of the fluids which have been added to it, either during the process of collection, at the time of packing, or later.

SUMMARY.

Pollen may be collected by the worker bee upon its mouthparts, upon the brushes of its legs, and upon the hairy surface of its body. When the bee collects from small flowers, or when the supply is not abundant, the mouthparts are chiefly instrumental in obtaining the pollen.

The specialized leg brushes of the worker are used to assemble the pollen, collecting it from the body parts to which it first adheres and transporting it to the pollen baskets or corbiculæ of the hind legs. In this manipulation the forelegs gather pollen from the mouthparts and head; the middle legs, from the forelegs and from the thorax; the hind legs, from the middle legs and from the abdomen.

The pollen baskets are not loaded by the crossing over of one hind leg upon the other or to any great extent by the crossing of the middle legs over the corbiculæ. The middle legs deposit their loads upon the

pollen combs of the hind plantæ, and the plantæ, in turn, transfer the pollen of one leg to the pecten comb of the other, the pecten of one leg scraping downward over the pollen comb of the opposite leg. (See fig. 7.) A little pollen is loaded directly from the middle legs into the baskets when these legs are used to pat down the pollen masses. (See fig. 6.)

Aside from the foregoing exception, all of the pollen which reaches the baskets enters them from below, since it is first secured by the pecten combs, and is then pushed upward by the impact of the rising auricles, which squeeze it against the distal ends of the tibiæ and force it on into the baskets to meet that which has gone before.

The long hairs which form the lateral boundaries of the baskets are not used to comb out pollen from the brushes of any of the legs. They serve to retain the accumulating masses within the baskets and to support the weight of the pollen, as it projects far beyond the surfaces of the tibiæ.

Pollen grains are moistened and rendered cohesive by the addition to them of fluid substances which come from the mouth. Analyses show that honey forms a large part of this moistening fluid, although nectar and secretions from the salivary glands are probably present also.

In the process of pollen manipulation this fluid substance becomes well distributed over the brushes of all of the legs. The forelegs acquire moisture by brushing over the mouthparts, and they transfer this to the hairs of the breast and to the middle-leg brushes when they come in contact with them. The middle-leg brushes transmit their moisture to the pollen combs of the hind legs when they rub upon them. All of these brushes also transport wet pollen which has come from the mouthparts and thereby acquire additional moisture. The auricles and the plantæ of the hind legs become particularly wet from this source, since fluid is squeezed from the wet pollen when it is compressed between the auricles and the distal ends of the tibiæ. Dry pollen which falls upon the body hairs becomes moist when brought into contact with the wet brushes or with wet pollen.

During the process of manipulation pollen passes backward from its point of contact with the bee toward its resting place within the baskets.

Pollen which the collecting bee carries to the hive is deposited by this bee within one of the cells of the comb. As a rule, this pollen is securely packed in the cell by some other worker, which flattens out the rounded masses and adds more fluid to them.

BIBLIOGRAPHY.

ALEFELD, Dr.—Vol. 5, Nos. 15 and 16, Eichstädt Bienen Zeitung. Summarized in "Die Bienenzeitung in neuer, geschichteter und systematische geordneter Ausgabe." Herausgegeben vom Schmid und Kleine: Erste Band, Theoretischer Theile. 1861.

CASTEEL, D. B., 1912.—The manipulation of the wax scales of the honey bee, Circular 161, Bureau of Entomology, U. S. Dept. Agriculture, pp. 15.

CHESHIRE, F. R., 1886.—Bees and bee-keeping; scientific and practical. Vol. I, scientific; II, practical. London.

FLEISCHMANN und ZANDER, 1910.—Beiträge zur Naturgeschichte der Honigbiene.

FRANZ, A., 1906.—In "Unsere Bienen," herausgegeben von Ludwig, A., Berlin. pp. [viii]+831.

HOMMELL, R., 1906.—Apiculture, Encyclopédie Agricola, Paris.

PHILLIPS, E. F., 1905.—Structure and development of the compound eye of the bee. Proc. Acad. Nat. Sci. Philadelphia, vol. 57, pp. 123–157.

SLADEN, F. W. L., 1911.—How pollen is collected by the social bees, and the part played in the process by the auricle. British Bee Journal, vol. 39, pp. 491–493, Dec. 14.

SLADEN, F. W. L., 1912.—(*a*) How pollen is collected by the honey bee. Nature, vol. 88, pp. 586, 587, Feb. 29.

1912.—(*b*) Further notes on how the corbicula is loaded with pollen. British Bee Journal, vol. 40, pp. 144, 145, Apr. 11.

1912.—(*c*) Pollen collecting. British Bee Journal, vol. 40, pp. 164–166, Apr. 25.

1912.—(*d*) How propolis is collected. Some further notes on pollen-collecting. Gleanings in Bee Culture, vol. 40, pp. 335, 336, June 1.

1912.—(*e*) Hind legs of the worker honey bee. Canadian Bee Journal, vol. 20, p. 203. July.

WOLFF, O. J. B., 1873.—Das Pollen-Einsammeln der Biene. Eichstädt Bienen-Zeitung. 29 Jahrg. Nrs. 22 u. 23, pp. 258–270.

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